AMPHIBIANS OF SOUTHEASTERN TANZANIA, WITH SPECIAL REFERENCE TO *STEPHOPAEDES* AND *MERTENSOPHRYNE* (BUFONIDAE)

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ABSTRACT. Records are given of 47 species of anurans collected in southeastern Tanzania. *Stephopaedes* and *Mertensophryne* are discussed at length; the two genera are provisionally regarded as being distinct on the grounds of differences in adult morphology, and diagnoses are given. Tanzanian material of *Stephopaedes* is described as a species distinct from the Zimbabwean *S. anotis*. *Mertensophryne m. micranotis* and *M. m. rondoensis* are found to be inseparable, and *schmidti* Grandison is excluded from this genus. *Stephopaedes* and *Mertensophryne* are apparently restricted to eastern African lowland forest and transitional lowland-Afromontane forest, now very fragmented. Most eastern Tanzanian species are assignable to an East African lowlands fauna, with characteristically enormous ranges. A set of widespread species with ranges centered more to the west is represented in more upland areas. There are relatively few endemic species.

INTRODUCTION

Southeastern Tanzania is here taken to be the region of Tanzania south of the Great Ruaha and Rufiji Rivers, and east of the highlands as demarcated by the 1,000 m contour. This area for the most part consists of the extensive Southeast Plateau, and a Coastal Hill Region (Berry, 1971). Alluvial lowlands occur along most of the northern limit. Rainfall in the region is in excess of 800 mm per annum (Berry, 1971), with the result that it is "a land closely covered, the cover varying from *miombo* woodland to light scrub" (Moffett, 1958: 220). The vegetation is characterized as "East African coastal mosaic" and "drier Zambezian miombo woodland" in the UNESCO/AETFAT/UNSO vegetation map (White, 1983). No portion of the Afromontane Region (*sensu* White, 1978) is included.

The area has been visited by several collectors, starting with Livingstone's expeditions of the 1860s, and followed notably by Loveridge, Ionides, and Rees. The material has been deposited mainly in the Museum of Comparative Zoology and the British Museum (Natural History). Much of this material was reviewed briefly by Poynton (1977), but subsequent taxonomic work in eastern and, especially, southern Africa (covered by Poynton and Broadley, 1985a, 1985b, 1987, 1988) calls for a more thorough review. In particular, southeastern Tanzania is the only region in Africa where small-sized bufonids currently assigned to *Mertensophryne* and *Stephopaedes* are now known to be sympatric. The taxonomy of these bufonids has become confused (Poynton and Broadley, 1988), making a detailed discussion appropriate in this paper.

As the area reviewed here includes the Selous Game Reserve, it is hoped that this paper will stimulate further study of the amphibian fauna of this still rather poorly investigated region. The paper is based on a reexamination of material in the Museum of Comparative Zoology and the British Museum (Natural History). The acronyms MCZ and BM are used in the text. Other acronyms used are: FMNH, Field Museum of Natural History, Chicago;

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NMZB, Natural History Museum of Zimbabwe, Bulawayo; ZMUC, Zoological Museum, University of Copenhagen. A response was not obtained from the National Museums of Kenya, Nairobi, regarding Tanzanian material reported by Loveridge (1955) to have been deposited there; this material is listed separately in the species lists.

The nomenclature adopted in this paper follows that of Frost (1985), apart from more recent published changes.

SYSTEMATIC LIST

FAMILY BUFONIDAE

Genus *Stephopaedes*

Stephopaedes Channing, 1978. Type by original designation: *Bufo anotis* Boulenger, 1907.

Channing (1978) based his monotypic genus on the then recently discovered tadpole of *Bufo anotis*, which he believed to be "strikingly different from all other *Bufo* tadpoles known worldwide" (1978:394). Knowledge of tadpoles of other African dwarf bufonids was at the time very poor; subsequently, the tadpole of *Mertensophryne micranotis* was shown by Grandison (1980) to be extraordinarily similar to the *S. anotis* tadpole. Grandison (1980) did note some differences between the *S. anotis* and *M. micranotis* tadpoles. She reported the presence of an infrarostrodont in *micranotis*, which was taken to contrast with the condition in *anotis*, described by Channing (1978:394) as "Infrarostrodont absent (or very reduced and not pigmented or keratinized)." But in twenty Gosner stage 34–35 *anotis* tadpoles recently collected by Broadley (NMZB 8452), the infrarostrodonts are well developed and blackened in all but one individual, where it is small, although strongly keratinized. Rostrodonts in *anotis* and *micranotis* do not differ at this stage. As Grandison has noted, the interrupted row of supraangular keratodonts in *anotis* is lacking in *micranotis*, and the rows of keratodonts are shorter in *micranotis;* but this seems related to the much smaller size of the *micranotis* tadpole, in conformity with the much smaller adult size (average length of stage 34–35 is 21 mm in *anotis*, 11 mm in *micranotis*). The "less pronounced and incomplete development of the 'crown'" reported by Grandison (1980:302) in the *micranotis* tadpole does not constitute a

striking difference between stage 34–35 tadpoles of both species, and could be attributed to the size difference. The difference in tail shape noted by Grandison is not well marked: the dorsal fin rises more steeply in stage 34 tadpoles (BM 1982.850) than is illustrated in her figure 3 of a *micranotis* stage 30 tadpole, and resembles the condition in *anotis*.

It seems clear that the discernable differences in external features of *anotis* and *micranotis* tadpoles of the same Gosner stage are minor, and cannot be taken in themselves as grounds for generic separation. Ecological features, whose importance Channing (1978) emphasized in the definition of genera, likewise provide no grounds for separating *anotis* from *micranotis* at the generic level. In separating *Stephopaedes* from *Bufo*, Channing (1978) placed emphasis on the finding that "*Stephopaedes anotis* is adapted to breed in forest pools . . . the tadpole is adapted by virtue of its crown to live in pools with low oxygen tensions" (Channing, 1978:396). Yet the work of Grandison (1980) and Grandison and Ashe (1983) shows the tadpole of *M. micranotis* to be similarly adapted. Evidence from tadpole morphology and ecology would, adopting Channing's generic criteria, therefore lead directly to placing *Stephopaedes* in the synonymy of *Mertensophryne*.

Yet, before taking such a step, evidence from adult morphology needs to be considered. In the following discussion, "*anotis*" is initially taken, in the original sense of *S. anotis*, to include material from southeastern Zimbabwe and adjoining Mozambique, as well as material from southeastern Tanzania, the latter material having been referred, with some reservations, to "*Bufo anotis*" by Loveridge (1955) and by Poynton (1977). Later in this paper, the Tanzanian material will be assigned to a separate species. This proposed separation at the species level will not affect the discussion of the validity of the genus.

The genus *Mertensophryne* was erected by Tihen (1960), who considered the diagnostic features to be: seven presacral vertebrae, separate sacrum and coccyx, extensively developed quadratojugals and palatines, and absence of the m. adductor longus. The presacral vertebrae of 39 *Stephopaedes* specimens have been examined by means of clearing and staining, dissection, and X rays. Eight presacral vertebrae have been found in each case, although considerable variation is shown in the separation of the transverse processes of the eighth vertebra and the sacrum, to the extent that the structures are closely applied on the one side of one specimen (NMZB 8505). But as the number of presacral vertebrae is seven or eight in the *M. micranotis rondoensis* type series (Grandison, 1978), a count of presacral vertebrae does not produce satisfactory characters.

In *Stephopaedes* the sacrum and coccyx are separated in specimens that have been cleared and stained, dissected, and where X-ray images are clear; but Grandison (1978) has reported much variation in this part of the skeleton of *Mertensophryne*, which once more leads to limited taxonomic usefulness.

The quadratojugals and palatines of *anotis* match Tihen's description of being "extensively developed"; in fact they are even more developed than they are in *micranotis:* the palatine, pterygoid, and quadratojugal form a continuous unit supporting the maxilla, and the quadratojugal is developed to the extent of cradling the maxilla in a deep groove, which is continued by a groove in the pterygoid. Support for the maxilla is continued by a flanged expansion of the palatine. The whole structure is further supported by the medial rami of the pterygoid being applied to the parasphenoid alae: in *micranotis*, the medial rami are very reduced, falling far short of the parasphenoid rami. This degree of development in *anotis*, especially the groove in the quadratojugal securing the end of the maxilla, is unusual; it possibly compensates for reduced ossification of the descending arm of the squamosal, noted by Grandison (1981), as well as for the

generally more robust skull, which indeed shows some ornamentation of the nasals, frontoparietals, and dorsal portion of the squamosal. The skull of *anotis* therefore appears to be substantially different from that of *micranotis*.

Regarding the m. adductor longus, the absence of which was taken by Tihen to be a feature of *Mertensophryne*, in *anotis* the muscle varies from being clearly lacking (which seems the usual state) to being present as a well-defined strip of muscle that leaves the anterior edge of the m. pectineus and joins the connective tissue sheath of the m. adductor magnus. As in the case of vertebral features, therefore, variation does not permit a clear separation between the two genera to be made on the basis of this character.

While most internal features selected by Tihen for diagnosing *Mertensophryne* therefore do not decisively exclude *anotis*, a number of differences seem noteworthy in the external features of the adults of the two. Particularly evident are the parotid glands of *anotis*, which are much wider than the width of the upper eyelid, and descend laterally to the level of the arm. In *micranotis* these glands are weakly developed, are narrower than the width of the upper eyelid, and have straight lateral edges. While much variation in the development and shape of the parotid glands is conventionally accepted within the genus *Bufo*, the condition in *Stephopaedes* seems to be unique. Other external features distinguishing *Mertensophryne* from *Stephopaedes* (and dwarf African toads in general) are: marked glandular swellings in the canthal region; shortened outer toe, reaching only halfway or less along the length of the proximal digit of the fourth toe; no distinct webbing between toes; large, well-separated, conical, and heavily keratinized spines on the first finger of breeding males; small spines present on the rim of cloacal tube in breeding males; males with cornified dorsal spines (skin of males is typically smoother than female skin in African dwarf bufonids, including *Stephopaedes*). Markings in *Mertensophryne* and *Stephopaedes* are radically different: as will be described below, a middorsal inverted V posterior to the occipital region is the commonest dark marking in *Stephopaedes*, whereas *Mertensophryne* has a longitudinally arranged pair of parallel stripes in this region.

Putting the available data together, it appears that *Stephopaedes* and *Mertensophryne* are primarily sylvicolous bufonids that oviposit in water-filled holes, such as between buttress roots, or treeholes, or snail shells (Grandison, 1980; Grandison and Ashe, 1983; Poynton and Broadley, 1988). This allows breeding to occur where surface water does not accumulate or flow for long above soil, a situation not uncommon in eastern African forests. In these forests, it may be noted, microhylid and arthroleptid terrestrial breeders tend to be major elements of the anuran fauna. The ecological adaptation of these bufonids is indicated morphologically by highly derived tadpole features, and by the possession of a cloacal tube which is deeply folded and which directs the vent markedly towards the ventral surface, a character likely to be associated with internal fertilization (Grandison and Ashe, 1983; Poynton and Broadley, 1988). Yet, as noted above, there appears to be considerable divergence in several adult features, which provide *Stephopaedes* and *Mertensophryne* each with some unique character states. Notable among these are: the presence in *Stephopaedes* of a particularly strong posterior maxillary support, the slightly exostosed roofing of the skull, and the broad, flattened parotid glands; in *Mertensophryne* the reduced outer toe, the large spines on the inner finger of the breeding male, and the generally more spiny condition of the male. Two diverging phyletic lines are therefore indicated by adult morphology.

This situation may be accommodated nomenclaturally by recognizing separate genera: *Stephopaedes* and *Mertensophryne*. Therefore, despite what is implied

by Channing's views, the present paper takes a conservative position of recognizing two separate genera, pending more complete ecological and morphological knowledge of African dwarf toads. Sight should not be lost of the fact that the life histories of many African dwarf toads are still unknown or very imperfectly known. Regarding morphological features, account has to be taken of complexities in the diagnosis of *Mertensophryne*, discussed below; account also has to be taken of the uncertain generic status of forms such as *Bufo melanopleura* Schmidt and Inger, and indeed, the very poor definition of *Bufo* as a whole.

For the time being, *Stephopaedes* may be characterized as possessing the following combination of characters. (1) Tadpoles with a "crown" of tissue encircling the eyes and nostrils, no gap in the mental papillae, possessing supra- and infrarostrodonts and four rows of keratodonts (supra-angular row interrupted). (2) Adults medium sized, distance from snout to urostyle tip in females up to 45 mm, males to 38 mm. (3) Eight presacral vertebrae; separate sacrum and coccyx with bicondylar articulation. (4) Large quadratojugal cradling the maxilla in a groove; palatine robust and prominently ridged. (5) Nasals, frontoparietals, and squamosals slightly exostosed. (6) Descending arm of squamosal not ossified, to ossified halfway down. (7) Medial ramus of pterygoid applied to parasphenoid, overlapping in anterior-posterior plane. (8) No columella or tympanum. (9) No, or only vestigial, m. adductor longus; well-developed m. tensor fasciae latae, inserting on m. cruralis at about one-third of its length. (10) Ovarian eggs reaching a size of 2.5 mm, pigmented at one pole, numbering about 85 per gravid female. (11) Opening of vent directed very markedly towards the ventral surface in both sexes, and lined by deeply folded integument, deep folding also present in lining of cloacal tube. (12) Breeding males with minute asperities on inner and upper surfaces of inner two fingers, occasionally also on inner palmar tubercle. (13) No tarsal fold. (14) Subarticular tubercles of fingers and toes doubled, two enlarged palmar tubercles present (but inner much smaller and may be only slightly larger than other palmar tubercles). (15) Toes with limited webbing; one to two phalanges of third toe free. (16) Outer toe extending beyond proximal phalanx of fourth toe. (17) Parotid glands considerably wider than width of upper eyelid, flattened, extending ventrally to level of upper jaw. (18) Dorsal skin of females with light-tipped spines that surmount warty bases, the larger warts bearing rosettes of spines; ventral surface with more densely packed spines, but not forming well-developed rosettes. Skin of males less spinose. Spines on individuals below length of about 32 mm tend to have pointed, keratinized tips. (19) Dark dorsal markings often lacking, especially in Zimbabwean material. A dark middorsal spot behind the occipital region is the most common marking, typically forming the apex of an inverted V whose arms follow the diverging inner margins of the parotid glands. Dark interorbital patches or a bar may be present, and sometimes a pair of sacral patches. Remaining areas over back may show relative lightening, especially in the parotid and sacral regions.

Stephopaedes differs from *Mertensophryne* notably in having wide parotid glands; toes with webbing; outer toe extending beyond proximal phalanx of fourth; breeding males with a dense covering of minute asperities on two fingers; quadratojugal possessing a deep groove into which the maxilla is slotted; medial ramus of pterygoid making contact with the parasphenoid; and in showing cranial exostosis, which is apparently unique among small-sized African bufonids. Differences in markings and in size may also be noted.

Turning now to variation within *Stephopaedes*, Loveridge (1955) and Poynton (1977) assigned southeastern Tanzanian material to *anotis* Boulenger, while remarking on some differences between this material and material from the type lo-

cality of *anotis* in southeastern Zimbabwe. Loveridge stated that ventral markings were lacking in the single specimen he had from Tanzania (although he noted that ventral markings showed variation in Zimbabwean material), while Poynton recorded differences in webbing, head width, and dorsal markings between Tanzanian and Zimbabwean material. Subsequently, more material has been examined from Chirinda Forest, the type locality of *anotis* in Zimbabwe, and from the nearby Dombe Forest in Mozambique; and more material from southeastern Tanzania has been examined in the Museum of Comparative Zoology and the British Museum (N. H.). The increased amount of material has revealed consistent differences between Zimbabwe–Mozambique and Tanzanian collections. In view of this, Poynton and Broadley (1988) restricted the acceptable range of *S. anotis* to southeastern Zimbabwe and adjoining Mozambique. The Tanzanian material requires a new name. It is here named to honor the memory of the late Arthur Loveridge, who first reported this form in Tanzania, and who made an unequalled contribution to the herpetology of East Africa. In honoring his memory, recognition is given to the support that the Museum of Comparative Zoology gave to Loveridge, and also the assistance that the museum has continued to give to subsequent work on eastern and southern African amphibians.

Stephopaedes loveridgei new species
Figures 1, 2

Bufo anotis, not Boulenger, 1907. Loveridge, 1955: 195; Poynton, 1977:39.

Holotype. A gravid female from Mahenge, Tanzania (8°41′S, 36°43′E, ca. 1,000 m) in the British Museum (Natural History), London (BM 1969.1492), collected at an unspecified date in 1964 by A. Rees.

Paratypes. Six specimens (a 39 mm female which has been cleared and stained with alizarin, and five juveniles) in the British Museum (N. H.) (BM 1969.1493 through 1969.1498) collected by Rees between 1963 and 1964 from Mahenge. The specimen cited by Loveridge (1955) is also regarded as a paratype: a female with immature ova in the Museum of Comparative Zoology (MCZ 27907) collected by C. J. P. Ionides from "Kilwa" (?Kilwa Kivinje, 8°45′S, 39°24′E), 25.viii.1950.

Other material. Five half-grown specimens (MCZ 29430 through 29434) collected by C. J. P. Ionides from Liwale (9°48′S, 37°56′E), 13 to 16.v.1957. One juvenile (BM 1988.184) from the Rondo Plateau (ca. 10°08′S, 39°12′E) collected by A. Braunlich, 13.xi.1988, and two gravid females (BM 1988.246 through 247) from Kiwengoma Forest Reserve (ca. 8°20′S, 38°56′E) collected by J. Kingdon, probably in 1989.

Diagnosis. Closely resembling *Stephopaedes anotis* (Boulenger, 1907), but differing therefrom in the reduced webbing (two phalanges of third toe free in *loveridgei*, one free in *anotis*); relatively smaller outer metatarsal tubercle (0.75 or less length of inner metatarsal tubercle in *loveridgei*, more than 0.75 length in *anotis*). Adult dorsal skin (at least of females) more spinose than in *anotis*, e.g., >45 spines on upper eyelid of *loveridgei* (<35 in *anotis*), clear rosettes of spines on upper surfaces of hind limbs of *loveridgei*, although weakly developed in the Kiwengoma Forest Reserve specimens (not developed in *anotis*). Covering of minute spines on lip of vent more strongly developed than in *anotis*. Dorsal markings usually strongly defined in *loveridgei* (weakly or not shown in *anotis*), while ventral markings are very reduced or absent (ventral freckling nearly always well developed over pectoral region in *anotis*).

Loveridge (1955) noted that the Kilwa specimen differed from typical *anotis* in lacking ventral markings; it also differs from *anotis* in the other characters listed in the diagnosis of *loveridgei*. Poynton (1977) distinguished Tanzanian from Zimbabwean material partly on the basis of a supposedly broader head in the former.

Figure 1. *Stephopaedes loveridgei* sp. n. Dorsal aspect of holotype BM 1969.1492, from Mahenge, Tanzania. Natural size.

Figure 2. *Stephopaedes loveridgei* sp. n. Dorsal aspect of paratype BM 1969.1493, from Mahenge, Tanzania. Natural size.

The currently available material shows allometry in the head width/body length relationship, the head becoming relatively narrower the longer the specimen (average head width/body length 37.5% at length of 27 mm, 35.5% at length of 37 mm). Tanzanian and Zimbabwean material form a single regression line.

Description of type material. Showing the features of the genus, as discussed above. Two phalanges of third toe free of main webbing, although edge of web very serrated, making determination imprecise. Outer metatarsal tubercle rounded, 0.75 or less length of inner. Adult dorsal skin (known only from females) densely covered with light-tipped spines which surmount small, warty bases; larger warts over lateral and urostylar areas and on dorsal surfaces of legs have rosettes of spines, otherwise the spines are single. Dense covering of minute conical asperities conspicuous on the lip of the vent, even in immature specimens of both sexes.

Markings (in alcohol): top of head, parotid glands and central region of back a light brown; darker brown laterally. A dark middorsal V-shaped marking in the scapular region, apex pointing anteriorly, arms usually continuing posteriorly to mark the inner margins of the parotid glands. Also a thin, often broken, dark interocular bar, and a pair of darker sacral spots. A fine light line overlying the urostyle. Dorsal markings are faintly shown in the holotype; the paratypes show the sacral, scapular, and interocular markings more clearly (Fig. 2). Ventral surface immaculate or with a single, elongated dark fleck in the anterior pectoral region. There are no regular ventral markings, nor the freckling typical of *S. anotis*.

Dimensions of holotype: body length from tip of snout to tip of urostyle 37.8 mm, body length from snout to vent 41.8 mm (specimen well hydrated), width of head 14.3 mm, length of tibia (folded) 14.9 mm, length of foot (including metatarsal tubercle) 13.9 mm. BM paratype 1969.1494 has a snout–urostyle length of 38.4 mm, head width of 13.6 mm; the remaining BM paratypes have a snout–urostyle length ranging from 26.9 mm to 31.2 mm. The MCZ paratype from Kilwa has a snout–urostyle length of 32.2 mm, head width of 12.6 mm.

Snout–urostyle lengths of other material: Liwale 24.1–29.5 mm, Rondo Plateau 30.4 mm, Kiwengoma Forest Reserve 34.3–35.0 mm.

Discussion. Males in breeding condition have yet to be described. As with *S. anotis*, and most African dwarf toad species, adult

males may be expected to have smoother skins than females. Digital asperities in breeding condition may be expected to be numerous and minute. The ovarian eggs in the holotype have a diameter of 2.5 mm, which is the same size as ovarian eggs in *anotis* (Poynton, 1964a). It can be expected that the course of development of the tadpole is similar to that of *anotis*. In view of the lack of detailed knowledge of the behavior of *anotis* adults, the relatively limited webbing of *S. loveridgei* adults cannot lead to very firm predictions about habitat preferences in this species. Loveridge (1955) reported that the Kilwa specimen was "taken during dry weather at the edge of a small lake." The *loveridgei* specimens from Mahenge were collected by Rees in "semi-montane type country" rising out of "*Pseudoberlina/Brachystegia* country" (Rees, pers. comm., 1963). It may be hoped that the new BM material will stimulate the gathering and publication of more ecological data.

As will be discussed under the zoogeographical section, the disjunct distribution pattern shown by *Stephopaedes* is not without parallel in forested regions of eastern Africa. Whether distributional gaps shown by upland and/or sylvicolous taxa are products of range retraction associated with Quaternary climatic cycles, or whether the gaps originate from some form of dispersal, has been a matter of debate among African biogeographers (Poynton, 1983, 1986), which still continues owing to the limited amount of relevant data (e.g., Harmsen, 1989). While the present taxonomic differentiation in *Stephopaedes* appears at first sight to be the result of vicariance, there is too little information regarding both the environmental history of southeastern Africa, and the phyletic history of African dwarf bufonids, to test a vicariance hypothesis.

Genus *Mertensophryne*

Mertensophryne Tihen, 1960. Type by original designation: "*Bufo (micranotis) rondoensis* Loveridge, 1942."

Tihen (1960) chose *Bufo micranotis rondoensis* as the type of *Mertensophryne;* he referred *M. m. micranotis* Loveridge (1925) to *Mertensophryne* only tentatively, as no specimens of this form were examined. Tihen also referred *Bufo ushoranus* Loveridge (1932) to *Mertensophryne*, seemingly in error, since Grandison (1972) has shown this taxon to be a synonym of *B. taitanus* Peters. Tihen evidently based his conception of *B. ushoranus* on material from the Upemba Park, Zaire, which was misidentified as *ushoranus* by Schmidt and Inger (1959) and subsequently renamed *Mertensophryne schmidti* by Grandison (1972). Improved knowledge of the morphology and ecology of East African dwarf bufonids, notably through the work of Grandison (1972, 1978, 1980), shows Tihen's diagnosis of *Mertensophryne* to be inadequate, and consequently raises questions about the correctness of his inclusion of *schmidti* (as *ushoranus*) in the genus.

There are in fact several features that distance *schmidti* from *micranotis:* large single palmar tubercle; outer toe not markedly reduced; very spinose skin, with ventral as well as dorsal rosettes; nuptial asperities consisting of clusters of very small horn-tipped spinules; cloacal opening not markedly directed ventrally; ova unpigmented. Grandison (1978) noted the presence of an accessory head to the m. adductor magnus of *schmidti*, lacking in *micranotis*, and, in correspondence, has drawn attention to extensive anterior development of the sphenethmoid, which, quite unlike the sphenethmoid of *micranotis*, reaches the palatal processes of the premaxillae. In correspondence she has also drawn attention to the presence of a vestigial columella in one of the *schmidti* paratypes (BM 1977.1211, which has been cleared and stained with alizarin), and to the presence of small eustachian tubes. These features have been confirmed by the present writer.

In external features, *schmidti* in fact shows closer resemblance to the sympatric

Bufo melanopleura Schmidt and Inger than to *micranotis*, notably in the single enlarged palmar tubercle, enlarged metatarsal tubercles, outer toe not reduced, presence of webbing, densely spinose skin, cloacal opening directed more posteriorly than ventrally, small eustachian tube openings. It is not suggested here that *schmidti* and *melanopleura* should be assigned together to a separate genus. The current lack of knowledge of the larval stages of *schmidti* and *melanopleura* is a particular obstacle to an elucidation of their phylogenetic position. Accordingly, *schmidti* is here assigned along with *melanopleura* to *Bufo* (in its currently loose sense); it then has the combination *Bufo schmidti* (Grandison, 1972), with the synonyms *B. ushoranus* Schmidt and Inger, 1959 (not Loveridge, 1932), *Mertensophryne ushoranus* Tihen, 1960, and *Mertensophryne schmidti* Grandison, 1972.

Mertensophryne is therefore considered here to include only one species, *micranotis* Loveridge, with a known distribution in eastern Kenya and Tanzania. The genus may be characterized by possessing the following combination of characters. (1) Tadpoles with a "crown" of tissue encircling eyes and nostrils, no gap in the mental papillae, possessing supra- and infrarostrodonts and three rows of keratodonts. (2) Adults small sized (snout to urostyle tip in gravid females 16 to 24 mm, mature males 16 to 22 mm). (3) Seven, occasionally eight, rarely six, presacral vertebrae; sacrococcygeal articulation usually monocondylar, occasionally bicondylar, rarely fused. (4) Quadratojugal long, extending length of pterygoid fossa, overlapped by the maxilla; palatine slender, lacking any pronounced ridge. (5) No cranial ornamentation. (6) Descending arm of squamosal not ossified. (7) Medial ramus of pterygoid very reduced, not making contact with parasphenoid. (8) No columella or tympanum. (9) No m. adductor longus; well-developed m. tensor fasciae latae. (10) Ovarian eggs reaching a size of 2 mm, faintly pigmented at one pole, numbering about 76 per gravid female. (11) Opening of vent directed very markedly towards the ventral surface in both sexes, and lined by deeply folded integument, deep folding also present in lining of cloacal tube; cloacal opening of breeding males with transitory spines. (12) Breeding males with large, well-separated, heavily keratinized nuptial spines. (13) No tarsal fold. (14) Subarticular tubercles of fingers and toes doubled, two enlarged palmar tubercles present (inner smaller and may be only slightly larger than other palmar tubercles). (15) Toes without definite webbing. (16) Outer toe reaching only halfway or less along proximal phalanx of fourth toe. (17) Parotid glands weakly developed, narrower than upper eyelids, outer edge straight. (18) Dorsal skin of males and females with minute, light-tipped spines surmounting small warts, only rarely forming rosettes; ventral surface with smooth, pavement-like warts, more columnar over posterior area. (19) Dorsal markings: dark, slightly raised areas which, when most complete, form a middorsal stripe on the snout, an oblique stripe over each eyelid, a patch between the posterior region of the eyelids, and three pairs of parallel, longitudinally arranged stripes in the occipital, postscapular and postsacral regions, the latter pair tending to become rounded as patches. Light patches may occur in the occipital area, and more commonly a pair of light sacral patches is developed, sometimes joining middorsally and continuing into a lightening of most of the area between the dark longitudinal stripes. A middorsal dark inverted V behind the occipital area, found in *Stephopaedes*, is not developed.

In the current poor state of knowledge of small-sized African bufonids, it cannot be said that *Stephopaedes* and *Mertensophryne* are more closely related to each other than either is to any other bufonid. Dubois (1986) has however grouped *Schismaderma* with *Stephopaedes* and *Mertensophryne* in a "tribe" mainly on account of perceived similarities between

structures on the dorsal surface of the tadpoles. The *Schismaderma* tadpole has a horseshoe-shaped fold extending from above the eyes to the trunk, and not enclosing the nostrils (Charter and MacMurray, 1939); whereas in *Stephopaedes* and *Mertensophryne* the "crown" encircles both nostrils and eyes. No homology in these structures can be maintained. Differences between the "saddle" of *Schismaderma* and the "crown" of *Stephopaedes* are shown clearly in the recent illustrations by Lambiris (1989).

Dubois also placed weight on Grandison's (1981) report of reduction in ossification of the squamosal in a "*vertebralis* group, which includes *Stephopaedes*, *Mertensophryne*, and possibly also *Schismaderma*" (pp. 208–209). The tentativeness expressed here regarding *Schismaderma* provides no grounds for supposing homology: indeed, Grandison (pers. comm., 1988) considers the squamosal in *Schismaderma* to be a "slender triradiate element that, in shape, is unique among the African bufonids." Taking into account the very marked differences between *Schismaderma* and the other two genera in egg size and number, and the tadpole and adult structure, behavior, and ecology, an exclusive grouping of *Schismaderma*, *Stephopaedes*, and *Mertensophryne* seems misconceived.

The "*vertebralis* group," which Grandison (1981:208) saw as including "all the medium and small sized toads that have double subarticular tubercles and occur in southern and eastern parts of Africa," contains many species that are still too poorly known to allow a phyletic analysis of the group. At the same time, new work is revealing variation—even within a single series of individuals—in features that at one time were taken to be definitive or diagnostic, such as the number of presacral vertebrae, the postsacral articulation, and the occurrence of the m. adductor longus. It seems premature at the moment to attempt to identify sister groups of *Stephopaedes* and of *Mertensophryne*. Such groups could be looked for among earless members of the large "*vertebralis* group" with two palmar tubercles, such as *Bufo lonnbergi* Andersson (Grandison, 1972; Poynton and Broadley, 1988). This is primarily a sylvicolous form. It is of possible significance that males of this species emit a mating call, even though otic structures are lacking (Tandy and Keith, 1972): the same is reportedly true of *Stephopaedes* and *Mertensophryne* (FitzSimons, 1939; Grandison and Ashe, 1983). *B. lonnbergi* has *Bufo*-like eggs and tadpoles, however (Stewart, 1967; Grandison, 1972).

Turning now to variation within *Mertensophryne*, Loveridge (1942) described *M. micranotis rondoensis* from just south of 10°S, separating it from the more northern *M. m. micranotis* "only in the throat being almost entirely white in the entire series, whereas in both sexes of *micranotis* . . . the throat is so heavily overlaid with black as to appear black." The *rondoensis* type series shows variation in gular pigmentation, and the presence of up to seven large flecks is not consistent with the description "almost entirely white." The throat of the holotype of *m. micranotis* is in turn not wholly pigmented. BM material from Pugu Forest, near Dar es Salaam (ca. 7°S), and from the Kiwengoma Forest Reserve, south of Utete (ca. 8°S), shows much variation in throat markings. Particularly notable is the variation shown in the four Kiwengoma F. R. specimens (BM 1988.242 through 245), collected about 230 km north of the type locality of *m. rondoensis:* the throat varies from being densely pigmented to being lightly flecked. In a specimen collected recently from the Rondo Plateau (BM 1988.184), five large flecks are present. It could hardly be said that there are clear indications even of a north-south cline in this feature, with the result that Loveridge's separation based on throat markings seems unworkable.

The *m. rondoensis* types are separable from the *m. micranotis* types on the basis of the minute size of their metatarsal tubercles, the diameter being less than the

width of the toe tips: in the *micranotis* types the diameter is greater than the diameter of the toe tips. MCZ and BM material from Zanzibar Island and from Kenya agree with *micranotis* in this respect. In the Pugu Forest material, recorded by Howell (1979, 1981) as *m. rondoensis*, the diameters of the tubercles and toe tips are about equal, while in the Kiwengoma F. R. series the diameter of the tubercles varies from being equal to being less than the diameter of the toe tips. A north-south cline therefore appears to be indicated in the relative size of the metatarsal tubercles, but it does not offer clear grounds for separating *m. rondoensis* from *m. micranotis*. A north-south cline may also exist regarding adult size: the snout–urostyle tip length is, so far, not known to exceed 18.2 mm in Rondo Plateau females, while Kenyan females may attain a length of 22 mm. The Kiwengoma F. R. series reaches a length of 19.5 mm. This again provides no means for clearly separating *m. rondoensis* from *m. micranotis*. No other features have been discerned that suggest any justification for retaining Loveridge's *rondoensis*.

Mertensophryne micranotis (Loveridge)

Bufo micranotis Loveridge, 1925:770.
Bufo micranotis rondoensis Loveridge, 1942:387. Tihen, 1960:266.

Records. Nchingidi, 823 m, "the name given to a clearing at the [Rondo] forest edge" (Loveridge, 1944) (MCZ), Rondo Plateau (BM), Kiwengoma Forest Reserve (BM).

Genus *Bufo*

Bufo Laurenti

Bufo gutturalis Power

Bufo gutturalis Power, 1927.
Bufo regularis, not Reuss, 1833. Loveridge, 1942:385; 1951:203; 1955:195. Poynton, 1977:39.

Records. Kilwa (MCZ), Kitaya (MCZ), Kivukoni (BM), Lindi (MCZ), Mahenge (BM), Mikindani (MCZ), Mtilangondo (BM), Rufiji River (7°47′S, 38°14′E) (BM). Liwale (Loveridge, 1955).

Bufo maculatus Hallowell

Bufo maculatus Hallowell, 1855 "1854."
Bufo pusillus Mertens, 1937. Poynton, 1977:39.

Records. Luwegu (BM), Mahenge (BM).

Bufo reesi Poynton

Bufo reesi Poynton, 1977:37.

Record. Merera (BM).

Bufo lindneri Mertens

Bufo lindneri Mertens, 1955. Clarke, 1989:298.

Record. Liwale District (BM).

Genus *Schismaderma*

Schismaderma Smith, 1849.

Schismaderma carens (Smith)

Bufo carens Smith, 1848. Loveridge, 1951:202; 1955: 195.

Records. Liwale (BM, MCZ).

FAMILY MICROHYLIDAE

Genus *Breviceps*

Breviceps Merrem, 1820.

Breviceps mossambicus Peters

Breviceps mossambicus Peters, 1854. Loveridge, 1942: 434. Poynton, 1977:39.

Records. Kilwa dist. (BM), Mahenge (BM), Mikindani (MCZ), Nchingidi (MCZ).

Genus *Phrynomerus*

Phrynomerus Noble, 1926.

Phrynomerus bifasciatus bifasciatus (Smith)

Brachymerus bifasciatus Smith, 1847.
Phrynomerus bifasciatus (Smith). Loveridge, 1942: 435; 1951:204; 1955:197. Poynton, 1977:39.

Records. Ifakara (BM), Kilwa (MCZ), Lindi (MCZ), Mahenge (BM). Liwale (Loveridge, 1955).

Genus *Spelaeophryne*

Spelaeophryne Ahl, 1924.

Spelaeophryne methneri Ahl

Spelaeophryne methneri Ahl, 1924. Loveridge, 1942: 434; 1955:197. Poynton, 1977:39.

Records. Litumba (MCZ), Mahenge (BM, NMZB), Matumbi (type locality: types not traced), Nchingidi (MCZ). Liwale (Loveridge, 1955).

FAMILY RANIDAE

Genus *Pyxicephalus*

Pyxicephalus Tschudi, 1838.

Pyxicephalus adspersus edulis Peters

Pyxicephalus edulis Peters, 1854.
Rana adspersa edulis (Peters). Loveridge, 1951:204; 1955:197.
Pyxicephalus adspersus, not Tschudi, 1838. Poynton, 1977:39.

Records. Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Mahenge (BM), Mikindani (MCZ), Tunduru (MCZ).

Discussion. Poynton and Broadley (1985b) tentatively accepted Parry's (1982) division of *P. adspersus* into three subspecies "until variation over the whole African range has been thoroughly investigated." In the material listed above, the ratio head width/snout–urostyle tip length varies from 50% (MCZ 25372, Kitaya) to 40% (BM 1969.1400, Kivukoni), a range which spans the ratios of all three supposed forms. This variation correlates with variation in pectoral markings to the extent that these markings tend to appear in material with relatively narrow heads, but they also occasionally appear in specimens with a width/length ratio of up to 44%, contrary to the <41% allowed in the diagnosis of *adspersus angusticeps* by Parry (1982) and Poynton and Broadley (1985b). These markings in southeastern Tanzanian juveniles are not as well developed as in the *adspersus angusticeps* type series from Beira. Regarding more northern Tanzanian material, it may be noted that MCZ 25379 from Amboni has a width/length ratio of 39% and well-developed gular and pectoral marking, placing it technically in *angusticeps*. This record seems geographically as anomalous as the "Shire Highlands" record reported in Poynton and Broadley (1985b). MCZ 59506 and 59507 from near Tabora, on the other hand, have some pectoral marking yet have width/length ratios of 47% and 49%, which are at the *a. adspersus* end of the *a. edulis* range. This is also true of MCZ 59395 from Kizumbe.

The light tympanic marking typical of *edulis* is not present in some specimens in the middle of the *edulis* width/length range (e.g., BM 1969.1402 and 1403 from Mahenge). Overall, it seems that this Tanzanian material does not give effective support to Parry's taxonomic analysis, and the assignation of the specimens listed above to *a. edulis* has again to be tentative.

Genus *Rana*

Rana Linnaeus, 1758.

Rana angolensis Bocage

Rana angolensis Bocage, 1866. Poynton, 1977:39.

Records. Kivukoni (BM), Mahenge (BM).

Genus *Hylarana*

Hylarana Tschudi, 1838.

Hylarana galamensis (Duméril and Bibron)

Rana galamensis Duméril and Bibron, 1841.
Limnodytes bravanus Peters, 1882.
Rana galamensis bravana (Peters). Loveridge, 1955: 196.
Hylarana galamensis bravana (Peters). Poynton, 1977: 39.

Records. Kihanzi/Kilombero (BM), Kilwa (MCZ).

Genus *Hildebrandtia*

Hildebrandtia Nieden, 1907.

Hildebrandtia ornata ornata (Peters)

Pyxicephalus ornatus Peters, 1878.
Rana ornata ornata (Peters). Loveridge, 1951:204; 1955:196.

Hildebrandtia ornata ornata (Peters). Poynton, 1977: 39.

Records. Kilwa (MCZ), Kivukoni (BM), Lindi District (MCZ), Liwale District (BM).

Genus *Ptychadena*

Ptychadena Boulenger, 1917.

Ptychadena oxyrhynchus (Smith)

Rana oxyrhynchus Smith, 1849.
Ptychadena oxyrhynchus (Smith). Poynton, 1977:39.

Record. Mkomangasha (BM).

Ptychadena anchietae (Bocage)

Rana anchietae Bocage, 1867.
Rana oxyrhynchus oxyrhynchus, not Smith, 1849. Loveridge, 1942:416; 1951:204; 1955:196.
Rana mascareniensis mascareniensis, not Duméril and Bibron, 1841. Loveridge, 1955:196 (part: MCZ 27918).
Ptychadena superciliaris, not Günther, 1848. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ifakara (BM), Kilwa (MCZ), Lindi District (MCZ), Mahenge (BM), Mbanja (MCZ), Mikindani (MCZ), Shughuli (BM), Tunduru (MCZ).

Ptychadena mascareniensis mascareniensis (Duméril and Bibron)

Rana mascareniensis Duméril and Bibron, 1841. Loveridge, 1942:417; 1955:196.
Ptychadena m. mascareniensis (Duméril and Bibron). Poynton, 1977:39.

Records. Boma Ulanga (BM), Kitaya (MCZ), Kivukoni (BM).

Ptychadena taenioscelis Laurent

Ptychadena taenioscelis Laurent, 1954. Poynton, 1977:39.
Rana mascareniensis mascareniensis, not Duméril and Bibron, 1841. Loveridge, 1951:204 (MCZ 26642).

Records. Ikulia (BM), Liwale (MCZ), Mkomangasha (BM).

Ptychadena mossambica (Peters)

Rana mossambica Peters, 1854.
Rana mascareniensis uzungwensis, not Loveridge, 1932. Loveridge, 1955:196.
Rana ansorgei, not Boulenger, 1905. Loveridge, 1955: 196.
Ptychadena upembae upembae, not Schmidt and Inger, 1959. Poynton, 1977:40.

Records. Kilwa (MCZ), Liwale (MCZ), Mbega (BM), Tunduru (MCZ).

Discussion. The Mbega specimen (BM 1969.1398) was assigned with some doubt to *upembae* rather than to *mossambica* by Poynton (1977) on the grounds of its relatively long feet. In other respects it does not agree with the current diagnosis of *upembae* (Poynton and Broadley, 1985b). The foot length in Mozambican material of *mossambica* rarely reaches 51% of the body length (snout–urostyle tip); the maximum is an exceptional 54% shown by a BM specimen from Caia, and also by the lectotype from Cabaceira, discussed by Poynton (1966). The feet of the Mbega specimen are 55% of the body length. This value falls within the range of *P. gansi* Laurent from Somalia, which is 53% to 57%. This range is also shown by BM material from the Kenyan lowlands. Lanza (1983) believes *gansi* to be "probably a synonym of *P. mossambica*," and this view would be supported if a cline in foot/body length between Kenya and Mozambique were to be demonstrated. The small amount of Tanzanian material listed above does indeed suggest the existence of an intermediate range of variation in that area. The MCZ specimen from Kilwa referred tentatively to *upembae* rather than to *mossambica* by Poynton (1977), on account of its relatively long feet, has a foot/body length of 52%, which is not unexpected for *mossambica* of southeastern Tanzania.

Somalian and Kenyan material agreeing with *gansi* differs from Mozambican material not only in foot length, but also to some extent in the markings on the hinder surface of the femur. Clear banding is usual in northern material; in southern material an irregular mottling is usual, but some individuals—including the *mossambica* lectotype (Poynton, 1966)—show distinct banding. Such individuals do not necessarily show the *gansi* character of longer feet: for example a specimen in a BM series from Beira has banded femora but a foot

length of 46% body length. The Mbega specimen shows irregular banding.

It seems likely that accumulating material will make it increasingly difficult to distinguish clearly between *mossambica* and *gansi*. The material listed above is accordingly assigned to *mossambica*.

Genus *Phrynobatrachus*

Phrynobatrachus Günther, 1862.

Phrynobatrachus natalensis (Smith)

Stenorhynchus natalensis Smith, 1849.
Phrynobatrachus natalensis (Smith). Poynton, 1977: 39.

Records. Mahenge (BM), Msolwa River (BM), Ruaha River (BM).

Phrynobatrachus acridoides (Cope)

Staurois acridoides Cope, 1867.
Phrynobatrachus acridoides (Cope). Loveridge, 1942: 421; 1955:197. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ikulia (BM), Kisanga (BM), Kitaya (MCZ), Luwegu (BM), Mahenge (BM), Mbega (BM), Mikindani (MCZ), Ruaha River (BM), Uga (BM). Tunduru (Loveridge, 1955).

Phrynobatrachus mababiensis FitzSimons

Phrynobatrachus mababiensis FitzSimons, 1932.
Arthroleptis minutus, not Boulenger, 1895. Loveridge, 1942:425.
Phrynobatrachus ukingensis mababiensis FitzSimons. Poynton, 1977:39.

Records. Lindi (MCZ), Maji ya Moto (BM), Mikindani (MCZ), Mwaya (BM), Riva Lumango (BM).

Discussion. This material shows some variation in the dilation of the tips of the toes, but it falls within the range of variation shown by a large MCZ series from Dar es Salaam, discussed by Poynton and Broadley (1985b:168).

FAMILY RHACOPHORIDAE

Genus *Chiromantis*

Chiromantis Peters, 1854.

Chiromantis xerampelina Peters

Chiromantis xerampelina Peters, 1854. Loveridge, 1951:203; 1955:195. Poynton, 1977:39.

Records. Boma Ulanga (BM), Kilwa (MCZ), Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Luhombero Kilombero confluence (BM), Mahenge (BM), Mikindani (MCZ), Morogoro (BM). Liwale (Loveridge, 1955).

FAMILY HYPEROLIIDAE

Genus *Leptopelis*

Leptopelis Günther, 1859 "1858."

Leptopelis flavomaculatus (Günther)

Hyperolius flavomaculatus Günther, 1864:310.
Leptopelis flavomaculatus (Günther). Poynton, 1977: 39.

Records. Mahenge (BM), Msolwa River (BM), Ruvuma (Rovuma) Bay (BM).

Leptopelis argenteus (Pfeffer)

Hylambates argenteus Pfeffer, 1892.
Leptopelis concolor, not Ahl, 1929. Loveridge, 1942: 390.
Leptopelis argenteus (Pfeffer). Loveridge, 1951:203.

Records. Mikindani (MCZ), Ruponda (MCZ). Lindi (Schiøtz, 1975).

Discussion. The two Mikindani specimens collected by Loveridge still have tails and are badly desiccated. They do however appear to be *argenteus*. Schiøtz (1975) used trinomials for *argenteus*, considering *concolor* Ahl to be subspecifically related on account of similar morphology, call, and habitat preference. No sign of intergrading was found, however. In view of the exceptional taxonomic difficulties encountered in *Leptopelis*, emphasized by Poynton and Broadley (1987), it is considered inadvisable to use the subspecific category in the genus unless problems caused by intergrading make its use unavoidable.

Genus *Kassina*

Kassina Girard, 1853.

Kassina maculata (Duméril)

Hylambates maculatus Duméril, 1853. Loveridge, 1942:394; 1951:203.

Records. Kitaya (MCZ), Liwale (MCZ), Ruvuma (Rovuma) Bay (BM).

Kassina senegalensis (Duméril and Bibron)

Cystignathus senegalensis Duméril and Bibron, 1841.
Kassina senegalensis (Duméril and Bibron). Loveridge, 1942:395; 1951:203. Poynton, 1977:39.

Records. Kitaya (MCZ), Kivukoni (BM), Lindi District (MCZ), Mahenge (BM), Mbalu River (BM).

Discussion. Of the material examined, only BM 1969.1475 and 1476 from Mbalu River have unbroken stripes of the "*argyreivittis* pattern" (Poynton and Broadley, 1987). Other material examined has the broken "Form 3 pattern" (Schiøtz, 1975) on one or both sides of the body. The Mahenge and Lindi District material has however been mislaid or discarded.

Genus *Afrixalus*

Afrixalus Laurent, 1944.

Afrixalus brachycnemis (Boulenger)

Megalixalus brachycnemis Boulenger, 1896.
Afrixalus p. pygmaeus, not Ahl, 1931. Schiøtz, 1975: 87. Poynton, 1977:39 (part: Mahenge).
Afrixalus brachycnemis (Boulenger). Poynton and Broadley, 1987:187.
?*Afrixalus septentrionalis morerei* Dubois, 1985.

Record. Mahenge (BM).

Discussion. As noted in Poynton and Broadley (1987), the small-sized forms of *Afrixalus* do not have constantly defined diagnostic characters, and their taxonomic treatment has been subject to confusion. According to the criteria adopted by Poynton and Broadley (1987), BM 1969.1280 from Mahenge clearly shows the characters to be expected of a male *brachycnemis*. This is not true of a smaller male, 1969.1279 from the same locality, but it is assumed to be the same species.

A. septentrionalis morerei is a replacement name of *A. pygmaeus* (Ahl) (Dubois, 1985). Schiøtz (1974, 1975) applied the name *A. pygmaeus* Ahl with uncertainty to a form which Poynton and Broadley (1987) believed corresponded with the syntypes of *brachycnemis*. The holotype of *pygmaeus* Ahl has not been directly compared with the *brachycnemis* syntypes, but if it is confirmed that *pygmaeus* Ahl and *pygmaeus* Schiøtz are conspecific, and also synomyms of *brachycnemis* Boulenger, then *septentrionalis morerei* would belong to the same synonymy.

Afrixalus species

Megalixalus brachycnemis, not Boulenger, 1896. Loveridge, 1951:203.
Afrixalus brachycnemis, not Boulenger, 1896. Schiøtz, 1975:84.
Afrixalus sp. Poynton and Broadley, 1987:189.

Records. Liwale District (MCZ), Ruaha River (BM), Sonjo (BM).

Discussion. The single females from Liwale District and from Ruaha River, and the immature specimen from Sonjo, do not present the features necessary for confident diagnosis.

Afrixalus crotalus Pickersgill

Megalixalus brachycnemis, Loveridge, 1942:398.
Afrixalus crotalus Pickersgill, 1984.

Records. Kitaya (MCZ), Mikindani (MCZ).

Afrixalus wittei (Laurent)

Megalixalus wittei Laurent, 1941.
Afrixalus wittei (Laurent). Poynton, 1977:39.

Record. Mbega (BM).

Discussion. In this specimen, the right paravertebral dark band fails to meet its opposite anteriorly on the head, and a fine median dark line runs from the tip of the snout to the tip of the urostyle. More material is needed to determine whether the anterior pattern signifies any intergrading with *A. quadrivittatus* (Werner), discussed by Schiøtz (1975).

Afrixalus fornasinii (Bianconi)

Euchnemis fornasinii Bianconi, 1850.
Megalixalus f. fornasinii (Bianconi). Loveridge, 1942: 395; 1951:203.
Afrixalus f. fornasinii (Bianconi). Loveridge, 1955: 195. Poynton, 1977:39.

Records. Kilwa (MCZ), Kisaye (BM), Kitaya (MCZ), Kugota (BM), Liwale (MCZ), Tunduru (MCZ).

Discussion. The BM Kugota specimen has no dorsal markings, a condition described by Loveridge (1955) in his Kilwa series, and discussed by Schiøtz (1975)

Genus *Hyperolius*

Hyperolius Rapp, 1842.

Hyperolius tuberilinguis Smith

Hyperolius tuberilinguis Smith, 1849. Poynton, 1977: 39.
Hyperolius citrinus citrinus, not Günther, 1864. Loveridge, 1942:407.
Hyperolius concolor tuberilinguis Smith. Loveridge, 1955:195.

Records. Ifakara (BM), Kisanga (BM), Kitaya (MCZ), Mahenge (BM), Mikindani (MCZ), Tunduru (MCZ).

Hyperolius pictus Ahl

Hyperolius pictus Ahl, 1931. Poynton, 1977:39.

Record. Kihanzi/Kilombero (BM).

Discussion. The single specimen from this locality is placed in the highly variable *pictus* with some uncertainty. Confirmatory material is desirable, since the altitude of ca. 240 m is low for this more typically upland species.

Hyperolius quinquevittatus quinquevittatus Bocage

Hyperolius quinquevittatus Bocage, 1866.
Hyperolius puncticulatus subsp. Loveridge, 1955:196.

Record. Tunduru (MCZ).

Discussion. This 27.2 mm female is hardly mistakable. It extends the known range of this form eastwards.

Hyperolius argus Peters

Hyperolius argus Peters, 1854.

Hyperolius ahli Loveridge, 1936. Loveridge, 1942: 404.

Record. Kitaya (MCZ).

Hyperolius puncticulatus (Pfeffer)

Rappia puncticulata Pfeffer, 1893.
Hyperolius puncticulatus (Pfeffer). Poynton, 1977: 39.

Records. Boma Ulanga (BM), Mahenge (BM).

Hyperolius mitchelli Loveridge

Hyperolius mitchelli Loveridge, 1953. Poynton, 1977: 39.

Record. Mahenge (BM).

Discussion. According to Rees's field notes, the *mitchelli* series was collected in January 1963; the *puncticulatus* material was collected in various months, but not between December and February.

Hyperolius pusillus (Cope)

Crumenifera pusilla Cope, 1862.
Hyperolius pusillus (Cope). Loveridge, 1942:412.

Record. Kitaya (MCZ).

Hyperolius nasutus Günther

Hyperolius nasutus Günther, 1864. Loveridge, 1942: 411. Poynton, 1977:39.

Records. Ilonga (BM), Kitaya (MCZ), Kipera (BM), Luheya (BM), Mahenge (BM), Msita (BM).

Discussion. Loveridge's Kitaya material, as currently preserved, is not nasute. However, a reading of Loveridge's comments (1942:411) makes it difficult to assign the material to anything but *nasutus*.

Hyperolius parkeri Loveridge

Hyperolius parkeri Loveridge, 1933.
Hyperolius parkeri rovumae Loveridge, 1942:410; 1955:196.

Records. Kilwa (MCZ), Kisaye (BM), Kitaya (MCZ).

Hyperolius reesi Schiøtz

Hyperolius sp. Poynton, 1977:39.

Hyperolius viridiflavus reesi Schiøtz, 1982:272.

Records. Boma Ulanga (BM), Ifakara (ZMUC), Magombero Forest (ZMUC), Mbega (BM).

Discussion. Specific status for this form is preferred in this paper, in view of reservations or disagreement expressed by Duff-MacKay (1980), Laurent (1983), Poynton (1985) and Poynton and Broadley (1987) regarding Schiøtz's (1975) assignation of many forms, including his *reesi*, to *viridiflavus*. Schiøtz (1982) believed, probably correctly, that *reesi* is most closely related to *H. mariae* Barbour and Loveridge from northeastern Tanzania and southeastern Kenya, but his placing of *mariae* as a subspecies of *viridiflavus* can again be viewed with doubt. Schiøtz (1975) himself noted many pecularities shown by *mariae*, and thought it "tempting to regard it as a full species." The relationship between *reesi* and *mariae* might be clarified by investigating the gap between their known ranges.

Hyperolius marmoratus marginatus Peters

Hyperolius marginatus Peters, 1854. Poynton, 1977: 39.

Records. Ilonga (BM), Luwegu (BM).

Discussion. The identification is based on a typically marked young adult from Ilonga. Two juveniles from this locality and two juveniles from Luwegu are assigned with some uncertainty to this form, since the markings are not distinct. It is perhaps noteworthy that this usually common reedfrog has been so poorly collected. The localities appear to be at the northeastern edge of the range of *H. marmoratus* as a whole, and information about population sizes and densities would be valuable.

Hyperolius marmoratus subspecies

Hyperolius undulatus, not Boulenger, 1901. Loveridge, 1942:402.

Hyperolius flavomaculatus, not Günther, 1864. Loveridge, 1942:403.

Hyperolius sp. Loveridge, 1951:203.

Hyperolius viridiflavus ssp. Schiøtz, 1975:215.

Records. Kitaya (MCZ), Liwale District (MCZ).

Discussion. According to the MCZ catalogue, Kitaya and Liwale material was identified as *marmoratus* subspecies by Laurent. The Kitaya material which Loveridge (1942) listed as *flavomaculatus* was assigned by Schiøtz (1975) to *H. viridiflavus*. Reasons for treating marmorate reedfrogs in the southern third of Africa as *marmoratus* rather than *viridiflavus* have been given by Laurent (1983), Poynton (1985) and Poynton and Broadley (1987).

Schiøtz (1975) suggested that the name *citrinus* Günther is available for Kitaya material, should Loveridge (1942) have been correct in interpreting Günther's "Zambezi Expedition" locality for *citrinus* as Ruvuma (Rovuma) Bay, rather than the Zambezi-Shire Basin. Examination of the BM accessions register gives no confirmation of Loveridge's preference for Ruvuma Bay. It appears that only two amphibian species are specifically entered as being from Ruvuma Bay: 64.19.48 (*Kassina maculata*) and 64.19.49 (*Leptopelis flavomaculatus*). *H. citrinus* Günther was tentatively treated as a synomym of *taeniatus* Peters by Poynton (1964a) and Poynton and Broadley (1987). The material listed as *citrinus* by Loveridge (1942: 407) from the Ruvuma (MCZ 25240 through 45, Kitaya) is *tuberilinguis* (Loveridge, 1955:195).

The Liwale material and MCZ 25299 from Kitaya are brown-colored juveniles with no clear markings. MCZ 25201 through 204 from Kitaya show adult markings which, although not well preserved, seem most similar to those of *marmoratus nyassae* Ahl, discussed by Poynton and Broadley (1987). But as the markings of this form are indefinite and very variable, particular caution is needed when assigning material to it. Identification of the Kitaya and Liwale material will have to await better knowledge of the marmorate reedfrogs of northern Mozambique and southern Tanzania.

FAMILY ARTHROLEPTIDAE

Genus *Arthroleptis*

Arthroleptis Smith, 1849

Arthroleptis stenodactylus Pfeffer

Arthroleptis stenodactylus Pfeffer, 1893. Poynton, 1977:39.
Arthroleptis stenodactylus loennbergi Nieden, 1915. Loveridge, 1942:430.

Records. Boma Ulanga (BM), Kitaya (MCZ), Kitikale (BM), Liage (BM), Lindi (MCZ), Mahenge (BM), Masasi District (MCZ), Mbanja (MCZ), Mikindani (MCZ), Mwaya (BM), Nchingidi (MCZ). Liwale (Loveridge, 1955).

Arthroleptis xenodactyloides Hewitt

Arthroleptis xenodactyloides Hewitt, 1933. Poynton, 1977:39.
Arthroleptis xenodactylus, not Boulenger, 1901. Loveridge, 1942:426.

Records. Mahenge (BM), Mikindani (MCZ), Nchingidi (MCZ).

FAMILY HEMISOTIDAE

Genus *Hemisus*

Hemisus Günther, 1859 "1858."

Hemisus marmoratus marmoratus (Peters)

Engystoma marmoratum Peters, 1854.
Hemisus marmoratum marmoratum (Peters). Loveridge, 1942:432, 1951:204, 1955:197. Poynton, 1977:39.

Records. Boma Ulanga (BM), Ilonga (BM), Kitaya (MCZ), Kivukoni (BM), Lindi (MCZ), Liwale (MCZ), Luhombero (BM), Mikindani (MCZ), Mlahi (BM).

FAMILY PIPIDAE

Genus *Xenopus*

Xenopus Wagler, 1827.

Xenopus muelleri (Peters)

Dactylethra muelleri Peters, 1844.
Xenopus muelleri (Peters). Poynton, 1977:39.

Records. Boma Ulanga (BM), Gunguli (BM), Kivukoni (BM).

ZOOGEOGRAPHY

Southeastern Tanzania falls within the range of what has been termed an East African lowland amphibian fauna (Poynton, 1962, 1990; Schiøtz, 1976). The latitudinal range covered by this fauna is enormous, the most widespread species extending a distance of over three thousand kilometers from Somalia to South Africa. Of the 47 species listed in this paper, 29 (62%) have a range of at least 2,000 km along the lowlands: *Bufo gutturalis, B. maculatus, Breviceps mossambicus, Phrynomerus bifasciatus, Pyxicephalus adspersus, Hylarana galamensis, Hildebrandtia ornata, Ptychadena oxyrhynchus, P. anchietae, P. mascareniensis, P. mossambica, Phrynobatrachus acridoides, P. mababiensis, Chiromantis xerampelina, Leptopelis flavomaculatus, Kassina maculata, K. senegalensis, Afrixalus fornasinii, Hyperolius tuberilinguis, H. argus, H. mitchelli, H. pusillus, H. nasutus, H. parkeri, H. marmoratus, Arthroleptis stenodactylus, A. xenodactyloides, Hemisus marmoratus*, and *Xenopus muelleri. Afrixalus crotalus* may prove to be assignable to this group; it has a known coastal range of some 1,300 km (extending southwards to the Beira area), but the true range may be underestimated on account of taxonomic confusion regarding northern Tanzanian material. The species may turn out to have a typical East African lowland range.

In contrast, *Stephopaedes loveridgei, Bufo reesi, Spelaeophryne methneri*, and *Hyperolius reesi* are known only from southern Tanzania, although the very poor state of collecting in northern Mozambique allows nothing to be said about their limitation southwards. This is also true of *Leptopelis argenteus*, currently known only from Tanzania (Poynton and Broadley, 1987). *Mertensophryne micranotis*, known to occur northwards into Kenya (Grandison and Ashe, 1983), may also extend into northern Mozambique, as does *Bufo lindneri* (Clarke, 1989).

Two treefrogs listed in this paper belong to what Schiøtz (1976) has described as a more western group, with ranges extending across central Africa south of the Congo forest block and its extension into southwestern Kenya. These are *Afrixalus wittei* and *Hyperolius q. quinquevittatus*. Likewise, the wide-ranging *Schismaderma carens*, *Rana angolensis*, *Ptychadena taenioscelis*, and *Phrynobatrachus natalensis* tend to avoid the extreme eastern lowlands, and could be included in a group centered in the interior of the continent (Poynton and Broadley, 1991). Less widespread, but with ranges centered west of southeastern Tanzania, are *Afrixalus brachycnemis*, *Afrixalus* sp., *Hyperolius pictus*, *Hyperolius marmoratus marginatus*, and also *Hyperolius puncticulatus*, although according to current taxonomy, this latter species reaches the coast in northern Tanzania, as discussed in Poynton and Broadley (1987).

The *Hyperolius marmoratus* subspecies from Kitaya and Liwale District cannot receive zoogeographical treatment on account of taxonomic uncertainty and paucity of records. The meagre two records of *H. marmoratus marginatus* allow little to be said about the distribution of the *marmoratus* group as a whole in southeastern Tanzania; but the available records suggest that *H. marmoratus* reaches its northern limit in the area around 8°30′S, in the Luwegu Basin. The southernmost record of *Hyperolius reesi* is at about the same latitude in the Kilombero Basin; if this species is affiliated to the *H. viridiflavus* group, the record indicates the southern limit of the group as a whole. The possibility of sympatry between the *marmoratus* and *viridiflavus* groups could be investigated around the junction of the Kilombero and Luwegu Rivers.

The presence in southeastern Tanzania of the northern *H. viridiflavus* and the southern *H. marmoratus* groups serves to emphasize the zoogeographical richness of the area, as does the presence of the Kenyan–Tanzanian *Mertensophryne* and Tanzanian–Mozambican–Zimbabwean *Stephopaedes*. This richness has tended to be undervalued, perhaps largely on account of the attractiveness of the Afromontane areas of Tanzania.

As "southeastern Tanzania" is taken in this paper to be an area below the 1,000 m contour, the Afromontane Region as described by White (1978) is excluded from it. Species which, according to White's treatment, would be classified as "marginal intruders" from the Afromontane Region could be expected to occur in more elevated areas of southeastern Tanzania, notably the widespread *Strongylopus fasciatus* (Poynton, 1964b), but the only record of a species which can be considered essentially "Afromontane" is the somewhat uncertain identification of a specimen of *Hyperolius pictus*.

The gap of some 1,400 km between the known ranges of *Stephopaedes loveridgei* and *S. anotis* is of the same order as the "Malawi interval" noted by White (1978) to occur in the distribution of several kinds of Afromontane plants. The known range of *S. loveridgei* does however lie below the Afromontane Region as defined by White, as does the range of *S. anotis:* the Chirinda Forest of Zimbabwe in which *anotis* occurs, lying between 1,076 and 1,250 m, is considered by White (1978:484) to be "transitional between Afromontane and lowland forest." Populations of *S. loveridgei* and of *Mertensophryne micranotis* may be considered to inhabit relicts of a formerly more widespread and continuous East African lowland forest, generally believed (e.g., Hamilton, 1976; Coetzee and van Zinderen Bakker, 1989) to have occurred in eastern Tanzania and Kenya during both glacial and optimal interglacial times. The lowland forest contributing to the more southern Chirinda and Dombe Forests is generally considered to belong to the same phytochorion as the East African lowland forest, but an interruption in this phytochorion is usually thought to occur north of the Zambezi Delta (Werger, 1978), which may offer a starting point in

accounting for the apparent vicariation within *Stephopaedes*.

Occupying the same area and habitat as both species of *Stephopaedes* are *Leptopelis flavomaculatus* and *Arthroleptis xenodactyloides* (Poynton and Broadley, 1985a, 1987), but both these species have much more extensive ranges, which include Malawi. More information is needed about the ecology of *Stephopaedes*, in particular the selection of breeding sites, before the relatively restricted ranges of its two species can be accounted for; but, as with *Mertensophryne*, available evidence indicates a particularly close dependence on a strictly forest environment. *Leptopelis flavomaculatus* may prove to be less dependent on a forest environment, while *Arthroleptis xenodactyloides*, which occurs in open country in upland areas, is certainly less so (Poynton and Broadley, 1985a, 1991).

Although southeastern Tanzania has been less intensively collected than some other areas of the territory, notably Afromontane areas, an examination of species lists from surrounding areas suggests only few species that might have escaped sampling. The most obvious is *Ptychadena schillukorum* (Werner), a "secretive species, easily overlooked" (Stevens, 1974), discussed recently by Perret (1987). This species is known from Mozambique–Malawi to the Sudan. Two other species of *Ptychadena*, which belong to the widespread, more western group, could possibly occur in the area: *P. uzungwensis* (Loveridge) and (more likely) *P. guibei* Laurent. The absence of *Tomopterna* species is notable, but the area may be too moist to favor their occurrence. This could also be true of *Bufo garmani* Meek, which has a patchy distribution in East Africa; it could perhaps also be true of dwarf *Bufo* species, such as *B. taitanus* Peters. These species are however easily overlooked (Clarke, 1989), and should be searched for. The moist conditions should favor apodans, but no apodan species have so far been reported from the area. These amphibians are again easily overlooked, and should be searched for. As was noted in the introduction to this paper, the area includes the Selous Game Reserve, and it is hoped that the present study will stimulate further work on the amphibians of this relatively neglected part of Africa.

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GAZETTEER

Boma Ulanga	8 10 S 36 57 E
Gawiro	8 34 S 35 50 E
Gunguli	8 35 S 37 15 E
Ifakara	8 09 S 36 41 E
Ikulia	8 45 S 37 05 E
Ilonga	9 04 S 36 51 E
Kihanzi-Kilombero confluence	8 25 S 36 22 E
Kilwa (Kivinje)	8 45 S 39 24 E
Kitaya	10 40 S 40 11 E
Kipera	8 25 S 36 25 E
Kisanga	8 25 S 36 25 E
Kitikale	7 32 S 37 02 E
Kivukoni	8 11 S 36 42 E
Kiwengoma Forest Reserve	ca. 8 20 S 38 56 E
Kugota	7 51 S 38 25 E
Liage	8 18 S 37 05 E
Lindi	10 00 S 39 41 E
Liwale	9 46 S 37 56 E
Luheya	9 00 S 37 00 E
Luhombero-Kilombero confluence	8 25 S 37 12 E
Lukandi	8 48 S 36 50 E
Luwegu River	8 45 S 37 23 E
Magombero Forest	7 50 S 36 58 E
Mahenge	8 41 S 36 43 E
Maji ya Moto	7 40 S 37 30 E
Masasi	10 43 S 38 41 E
Matumbi	9 29 S 35 31 E
Mbanja	9 24 S 39 45 E
Mbalu River	8 40 S 36 55 E
Mbega	8 38 S 36 08 E
Merera	8 33 S 36 02 E
Mikindani	10 17 S 40 07 E
Mkomangasha	8 58 S 37 24 E
Mlahi	8 30 S 37 12 E

Msita	8 34 S 35 55 E	Ruaha River	7 56 S 37 52 E
Msolwa River	8 02 S 37 00 E	Ruponda	10 15 S 38 42 E
Mtilangondo	8 25 S 37 07 E	Ruvuma (Rovuma) Bay	10 26 S 40 29 E
Mwaya	8 55 S 36 51 E	Shuguli	8 32 S 37 23 E
Nchingidi	10 08 S 39 12 E	Sonjo	7 50 S 36 52 E
Riva Lumango	7 32 S 37 02 E	Tunduru	11 07 S 37 21 E
Rondo Plateau	ca. 10 08 S 39 12 E	Uga	8 33 S 35 50 E